

The influence of hydrologic restoration on the productivity of a bottomland forest in central Ohio

Christopher J. Anderson and William J. Mitsch

*Schiermeier Olentangy River Wetland Research Park, School of Environment and Natural Resources.
The Ohio State University*

Abstract

Change in forest productivity in response to hydrologic restoration was evaluated at a 5.2-ha bottomland hardwood forest in central Ohio. In June 2000, the bottomland forest was restored to approximate natural flooding by cutting three breeches in an artificial levee constructed between the river and the forest (north section) and a fourth breach along the natural river bank to augment flooding at the south section. Total aboveground net primary productivity (ANPP) was calculated for the two sections of the forest using estimated forest litterfall and wood production. No significant difference in mean ANPP for the north section ($807 \pm 86 \text{ g m}^{-2} \text{ yr}^{-1}$) and the south section ($869 \pm 56 \text{ g m}^{-2} \text{ yr}^{-1}$) was detected; however the north section was substantially more productive than a previous ANPP estimate conducted before restoration. A significant positive relationship was detected between ANPP and the number of days flooded during the year (October 2003 - September 2004) in each plot. Forest ANPP and wood production were also significantly related to total tree basal area and topographic variability. Tree ring-analysis was used to compare mean basal area increment (BAI) growth 10 years (1991-2000) before the restoration to the 4 years (2001-2004) after the restoration. No immediate shifts in BAI were detected; however based on prevailing trends before and after restoration, canopy trees in the south section showed a noteworthy increase in BAI during 2003 and 2004. This shift in the south section was primarily due to the prevalence of boxelder (*Acer negundo* L.), the dominant species in this section. Evaluating the 14-yr series of BAI for trees in the bottomland, a significant relationship was detected between the total number of days of high-flood conditions ($>154 \text{ m}^3 \text{ sec}^{-1}$) and mean BAI ($\text{cm}^2 \text{ yr}^{-1}$) based on a two-year flooding history.

Introduction

Bottomland hardwood forests are considered transitional ecosystems because they are influenced by adjacent rivers or streams and terrestrial land upslope. These forests are often highly productive because of the regular influx of nutrients, material and energy from adjacent waterways (Mitsch and Gosselink 2000). The effects of hydrology on riparian forest productivity have been the subject of several studies (Mitsch and Ewel, 1979; Brown and Peterson, 1983; Mitsch and Rust, 1984; Taylor, 1990; Tockner et al., 2000; Mitsch et al., 1991; Magonigal et al., 1997; Robertson et al., 2001) and most have concluded that periodic flooding

has an important influence on the productivity of these ecosystems. According to the subsidy-stress model (Odum et al., 1979), flooding can be beneficial or detrimental to the productivity of the system, depending upon the frequency, timing and duration of the flood events. The model indicates that for a forest at steady-state, periodic flooding provides a nutrient subsidy and thereby increases overall productivity compared to forests in nearby uplands (that do not benefit from the subsidy) or forests in more frequent standing water that can become physiologically stressed (Teskey and Hinckley, 1977a; Kozlowski, 1997). The benefit of surface water connections from the river to floodplains has been demonstrated along the Danube River in Austria where Tockner et al. (2000) found that floodplains in this region have the highest productivity when a connection between the river and the floodplain alternates between a 'disconnection phase' (because of low river water levels) and a 'seepage/downstream surface connection phase' where low energy inflows of water occur. In this study, the floodplain benefited from nutrient subsidies from the river, but water levels also subsided before long-term anoxic conditions occurred that could potentially stress the forest. Despite application of the subsidy-stress model in several studies, other studies have found that the highest productivity occurred in forested regions other than those periodically flooded. Brown and Peterson (1983) and Burke et al. (1999) found that permanently flooded zones rather than periodically flooded zones had higher productivity while Magonigal et al. (1997) found no difference between upland and periodically flooded forest productivity. The Magonigal et al. study supported an earlier model presented by Mitsch and Rust (1984) which holds that the potential benefits derived from periodic flooding are offset by the physiological stress induced by anaerobic soil conditions. Evaluating tree rings of three floodplain species along the Kankakee River in northeast Illinois, Mitsch and Rust (1984) did not find a relationship between radial growth and flooding duration but instead attributed tree growth to a combination of hydrologic and climatologic factors that can influence soil moisture.

In most bottomland forests, the larger, canopy-sized trees often provide the majority of forest production (Kimmins, 1987); therefore the response of this stratum to changes in hydrology will typically dictate overall forest-level productivity. Numerous tree species can be present in a bottomland community and it has been shown that different species will have different responses and tolerances to flooded conditions (Teskey and Hinckley, 1977b,

Kozlowski, 1997). For instance, Dudek et al. (1998) found different responses to hydrological cues when comparing the long term growth of a flood tolerant species (*Populus deltoides* Marsh.) and a flood intolerant species (*Juglans nigra* L.) growing in the same central Ohio bottomland forest used in this study.

Given the inconsistencies in bottomland responses to flooding, it has been suggested that more studies need to evaluate existing forests under a changing hydrology to elucidate the influence of hydrology (Conner, 1994; Megonigal et al., 1997). Our study was conducted to evaluate short-term forest responses to the hydrologic restoration in a bottomland hardwood forest at the Olentangy River Wetland Research Park (ORWRP) in central Ohio. The objectives of this study were to determine if: 1) the reconnection of the north section of the bottomland forest to the adjacent Olentangy River increased aboveground net primary productivity (ANPP) after four years, 2) flood frequency or other ecological conditions within the bottomland could be used to predict ANPP, 3) there has been a response (positive or negative) in the average or species annual radial growth rate of canopy trees since hydrologic restoration, and 4) the frequency of previous flood events could be used to predict tree radial growth.

Methods and materials

Study site

The 5.2-ha bottomland hardwood forest at the Olentangy River Wetland Research Park (ORWRP) is located along the Olentangy River, a 4th order river in central-Ohio USA. The ORWRP bottomland forest varies between 25-90 m wide, is approximately 730 m long, and was hydrologically restored starting in June 2000 (Fig. 1). Hydrologic restoration was conducted as partial wetland mitigation by the Ohio Department of Transportation for wetland impacts associated with a highway project in Columbus, Ohio. The north section of the bottomland forest was disconnected from river flooding by a constructed levee (up to 2-m high) that was built over 70 years ago (Cochran, 2001) and extended along a 250 m stretch of the river. Three breaches (Cuts #1-3, Fig. 1) were opened in the north section levee and river water now regularly flows into and out of this section of the bottomland during high river events. The levee only affected the north section of the bottomland. The south section of the bottomland was not restricted by artificial levees and periodically flooded by direct surface flow from the river; however floods were infrequent and only occurred during extremely high river events. To increase flood frequency and create flow-through conditions, a fourth breach (Cut #4) was made through the natural river bank to a lateral swale which extends through the south section (Fig. 1).

In a previous study of riparian forest productivity in this bottomland hardwood forest, forest productivity and the basal growth of canopy trees (>25cm dbh) were evaluated using data collected between 1998 and 2000 (Cochran, 2001).

Mean ANPP of the ORWRP bottomland (averaged between sections) was estimated at 800 g m⁻²yr⁻¹, substantially lower than productivity of two other unrestricted bottomlands upriver that averaged 1280 g m⁻²yr⁻¹. Higher productivity in the unrestricted bottomland forests was attributed to their ability to receive river influx and higher proportion of species adapted to these conditions.

Climate and hydrology

River stage has been measured twice nearly every day since 1994 using a permanent staff gauge immediately upriver from the ORWRP bottomland (Fig. 1). When water levels were high enough to flood portions of the bottomland, we observed the spatial extent of flooding within the forest relative to river stage and recorded observations in river inflow sources (Cuts #1-4), internal flow patterns, and relative depths at various river stages. Precipitation and weather data were gathered from a Columbus, Ohio weather station operated by the Ohio Agricultural Research & Development Center (www.oardc.ohio-state.edu/centernet/weather.htm).

Aboveground net primary productivity

To determine the effect of the restored hydrology on bottomland productivity, wood and litterfall production data were collected to determine annual aboveground net primary productivity (ANPP) (Newbould, 1967). A transect was established within the north and south sections of the forest. Transects were randomly established but designed to extend parallel to the river and through the regularly flooded portions of both sections. Because of the wider forest in the south section, parallel transects were used to increase plot replication. A total of 10 plots (20 m x 25 m) were measured and marked in the field (Fig. 2).

In each plot, all trees with a dbh (1.3m) >5cm were identified by species, tagged and measured for dbh in April 2004 and April 2005 to determine 1-yr basal increase. Using tree data, species importance values were calculated in 2004 using the following equation:

$$\text{Importance value} = \text{relative density} + \text{relative dominance} + \text{relative frequency} \quad (1)$$

The increase in tree basal area (A_i) (cm² yr⁻¹) was calculated by the following equation (Newbould, 1967):

$$A_i = p [r^2 - (r-i)^2] \quad (2)$$

Where, r = radius of tree at breast height (cm), and i = radial increment per year (cm² yr⁻¹)

Tree heights were measured using a clinometer in May 2005 and the annual wood production per tree (P_i) (g yr⁻¹) was calculated by the following parabolic volume equation (Whittaker and Woodwell, 1968; Phipps, 1979):

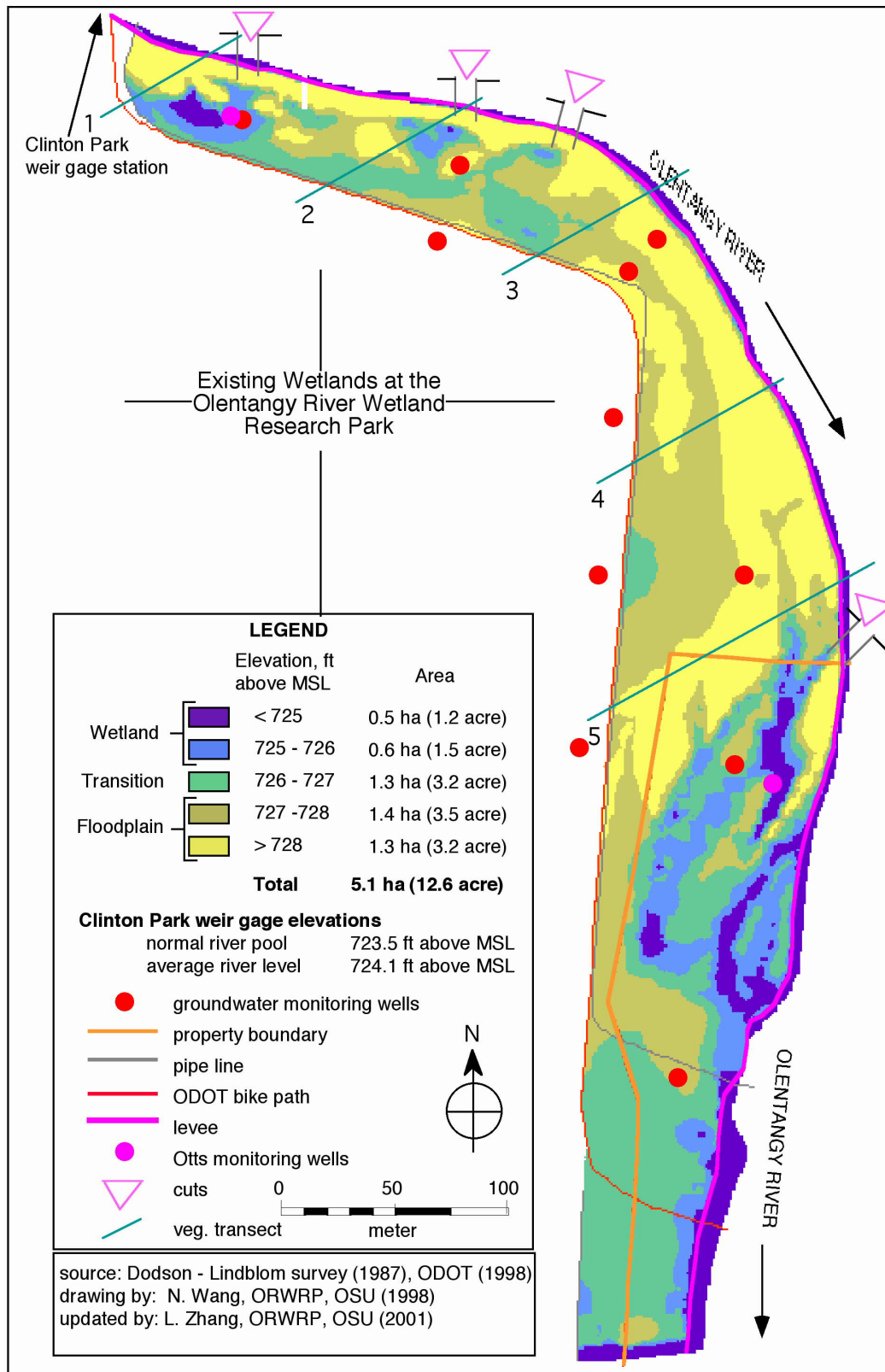


Figure 1. Map of the bottomland forest at the Olentangy River Wetland Research Park (ORWRP) at The Ohio State University in Columbus, Ohio, USA indicating site topography and levee breaches (Mitsch and Zhang 2004). Hydrologic restoration was conducted by breaching a levee (Cuts #1-3) along the north section and breaching the river bank at the south section (Cut #4).

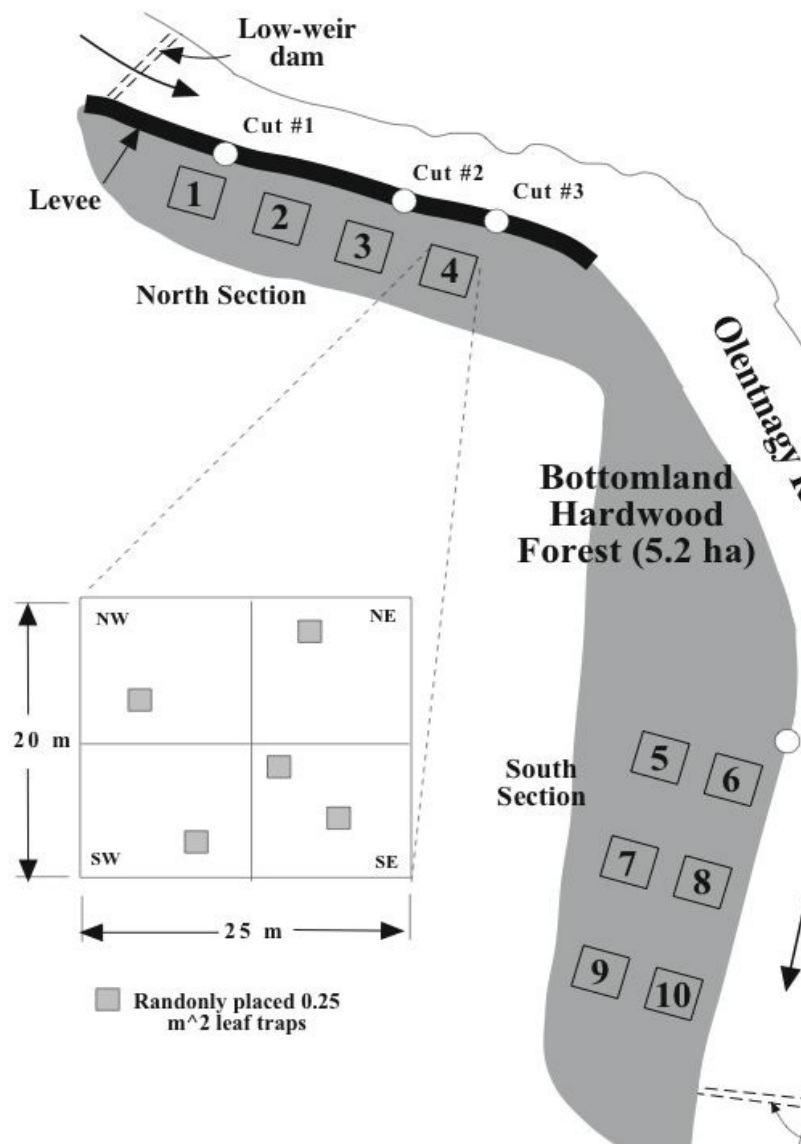


Figure 2. Experimental layout at the ORWRP bottomland hardwood forest indicating the location and dimensions of tree plots and litter traps. Each tree plot was divided into four quadrants (NW, NE, SW, and SE) for placement of random litter traps including a fifth trap near the plot center.

$$P_i = 0.5r A_i h \quad (3)$$

Where, r = wood specific gravity (g cm^{-3}), and h = tree height (m)

Wood specific gravity values were obtained from the U. S. Forest Products Laboratory (1974) and Alden (1995). The plot wood production was calculated as the summation of all wood production per tree and converted to $\text{g m}^{-2} \text{yr}^{-1}$.

A total of 50 leaf litter traps (5 per plot) were installed in May 2004. Each plot was divided into 4 quadrants and a leaf trap was randomly placed in each quadrant with a fifth

trap randomly placed near the center (Fig. 2). Leaf traps were 15 cm tall, 0.25 m^2 in area, lined with 2-mm screen and installed approximately 1.0 m off the ground to avoid flooding and litter saturation. Litterfall was collected for one year starting in May 2004. Traps were emptied twice a month from June-December and once a month from January-May. After each collection, the contents were separated into leaves, reproductive material and woody material, air-dried at room temperature for 1 week and then at 105°C for four days or until constant mass prior to being weighed. Leaf traps were averaged per plot and the summation of all fine litter production (leaf litter and reproductive materials) was

calculated. Because of vandalism and flood/ice damage, several sampling periods had plots with less than the 5 traps available and were averaged only using the plots that were undamaged.

Using litterfall and wood production data, aboveground net primary productivity (ANPP) ($\text{g m}^{-2} \text{yr}^{-1}$) for each plot was estimated using the following equation (Whittaker and Woodwell, 1968):

$$\text{ANPP} = \text{plot wood production} + \text{litterfall production} \quad (4)$$

Predicting ANPP, litterfall production and wood production

Various environmental parameters known to influence forest productivity were selected to predict forest productivity in 2004 (ANPP, wood production and litterfall) through linear regression. The 2004 river hydrograph and observations of flooded conditions at different river stages were used to determine 1) the number of flood events that directly connected to each plot, and 2) the number of days that the river had a surface water connection to each plot. Flooding frequencies and durations in 2004 for each plot were estimated for the preceding year (October 2003 - September 2004), preceding two years (October 2002 - September 2004) and the growing season (April - September 2004) and used for regression analyses.

To assess the potential influence of tree plot elevation on ANPP, the corners of each plot and each random leaf litter trap within the plot quadrants (Fig. 2) were surveyed for elevation using a TOPCON RL-H3CTM rotating laser level and the mean plot elevation (m MSL) was calculated. To assess the potential influence of topographic variability on forest productivity, the variance of all elevation points at each plot was also calculated and used to predict forest productivity.

Other data used as predictor variables included canopy cover and tree basal area. Canopy cover (%) was estimated for each plot in August 2004 using a convex spherical crown densitometer. Cover was measured at each trap facing the four cardinal directions and the mean of all measurements were calculated for the entire plot. Tree basal area ($\text{cm}^2 \text{m}^{-2}$) per plot was calculated based on the total basal area of all trees >5 cm dbh measured in April 2004.

Tree-ring analysis

For each forest canopy tree (>25 cm dbh and >15 m height) in the plots, two cores were extracted using a 5.15 mm inside increment borer. Seven supplemental trees located between tree plots (5 in the north section and 2 in the south section) were added. For comparison with trees not in the flood zone (the upland area between sections) a total 7 trees from species representative of the flooded sections were randomly selected for coring. For each tree, two cores were taken at 90 degree angles from each other to account for natural variation and were collected at least 12

cm into the tree to collect >15 years of increment growth. The cores were temporarily stored in straws, air-dried and then glued into grooved holders. Cores were sanded with a series of finer sandpaper grit (80-600) and polished with lamb's wool. Tree cores were scanned and the image was analyzed for tree-ring widths (to the nearest 0.01 mm) using WinDENDRO TM (2002). Replicate tree-ring increments were compared for comparable growth patterns, verified with a stereoscope when necessary and averaged for each tree.

Using the tree cores and tree diameter, basal area (A_i) increments (BAI) were calculated from 1991 to 2004. Years 1991-2000 were selected as representative pre-restoration growth and years 2001-2004 were analyzed as post-restoration years. Although most restoration work was conducted in June 2000, each cut was excavated further in early 2001. The first flood event to overflow into bottomland forest did not occur until April 2001. For comparison of trees between sections and species, the BAI ($\text{cm}^2 \text{yr}^{-1}$) from each tree were standardized to reflect percent basal increase relative to total tree basal area [BAI (%)], and were calculated using the following equation:

$$\text{BAI}(\%) = [(A_i \text{ Year } X - A_i \text{ Year } X-1) / A_i \text{ Year } X-1] * 100 \quad (5)$$

Predicting basal growth

The series of BAI data collected for 1991-2004 (both cm^2 and %) were evaluated to determine if flood stage (based on river discharge) could be used to predict basal growth. A discharge curve prepared for river depth at this section of the Olentangy River (Mitsch, 1995) was used to determine the number of bank-full flood days/events (221.2 mMSL or >70 $\text{m}^3 \text{sec}^{-1}$) and the number high-flood days/events (221.6 mMSL or >154 $\text{m}^3 \text{sec}^{-1}$) between March 1994 and September 2004. The high-flood discharge was selected because this is the discharge level that was likely required to directly flood both sections of the bottomland despite the presence of the levee. Daily river discharge data from an upstream United States Geological Survey (USGS) stream gauge (near Delaware, Ohio, Station No. 03225500) was used to estimate discharge rates at the study site between October 1990 and March 1994. A regression between known ORWRP and USGS discharge rates were used to estimate discharge on the days where no water level data was available at the study site ($\text{ORWRP} = 1.43 * \text{USGS} + 5.34$, $R^2 = 0.92$).

Using daily river discharge data, the frequency and duration of flood events were determined for each year (from 1 October in the preceding year to 30 September) and growing season (1 April to 30 September). Frequency and duration were determined for bank-full and high-flood discharge events. For both thresholds, the number of days and events in which these rates occurred were counted for each applicable year and growing season.

In addition to conducting a regression analysis on the concurrent flood and BAI data for a given year, regressions were also conducted to evaluate the possibility of a lag in

tree basal growth response to floods. A regression analysis was used to evaluate flood frequency and BAI data lumped into 2-yr increments. In addition to capturing potential lag effects, lumping BAI data in this manner has been suggested as an effective guard against potential errors due to false-rings or other measurement errors (Mitsch et al., 1991). A second regression analysis was conducted using two years of preceding river discharge data to predict the BAI for a given year.

Statistical analyses

An independent t-test was conducted to compare the mean ANPP between the north and south sections of the bottomland. Because litterfall and wood production have been shown to respond independently to environmental factors, independent t-tests were also conducted to compare these parameters. Analyzing tree-ring data, paired t-tests and trend analyses were used to compare BAI (%) between pre- and post-restoration years for each section. Similarly, paired t-tests and trend analyses were used to compare BAI (%) for pre- and post restoration specimens of *A. negundo* and *A. glabra*. All pre- and post-restoration data were tested for normality using the Kolmogorov-Smirnov test, homogeneity of variances using Levene's test, and transformed as needed to meet test assumptions. For all t-tests, p-values <0.05 were considered significant differences and p-values <0.01 were considered highly significant.

Regression analysis was used to evaluate relationships between forest productivity (ANPP, litterfall production and wood production) and measured environmental variables [flooding frequency (total year, total year + preceding year, and growing season), flooding duration (total year, total year + preceding year, and growing season), elevation, topographic variability, total tree basal area and canopy cover] at each plot. Best-fit regression analysis was conducted to determine the most appropriate model type (linear or polynomial). Significance of the regression

analyses were tested with analysis of variance with p-values <0.05 considered a significant and p-values <0.01 considered highly significant. All response and predictor variables were tested for normality using the Kolmogorov-Smirnov test and homogeneity of variances using Levene's test. Variables not meeting test assumptions were transformed as needed. Where the regression of time series data was conducted, an autocorrelation function (1 or 2-year lags), the Durbin Watson test, or both were conducted as appropriate. Minitab™ v.14 was used to run all statistical analyses.

Results

Hydrology and climate

Based on precipitation data and a hydrograph of the Olentangy River (Figs. 3 and 4), conditions in the post-restoration period tended to be wetter than normal. Between 1991 and 2000, there were only two years (1995 and 1996) where precipitation was exceptionally high (>20 cm above normal for any 3-month period) and one year (1999) where it was exceptionally low. In contrast, three out of four of the post-restoration years (2002 - 2004) had exceptionally wet seasons. However, these wet seasons were offset by drier than normal winter seasons. Nevertheless, frequent high river levels were common during those years. As indicated on the post-restoration river hydrograph (Fig. 4), river levels frequently met or exceeded the designed bottomland flood level (221.2 m MSL) from 2002-2004 compared to much less frequently in 2001. It was noted during this period that Plot #5 in the south section (Fig. 2) was too high in elevation to become regularly flooded (unlike all the other plots) and therefore it was removed as part of the south section and analyzed separately as an upland plot.

Floods tended to be short-term events and rarely lasted more than a few days. Flood waters tended to rapidly rise and then fall back to normal flow levels (220.6 m MSL).

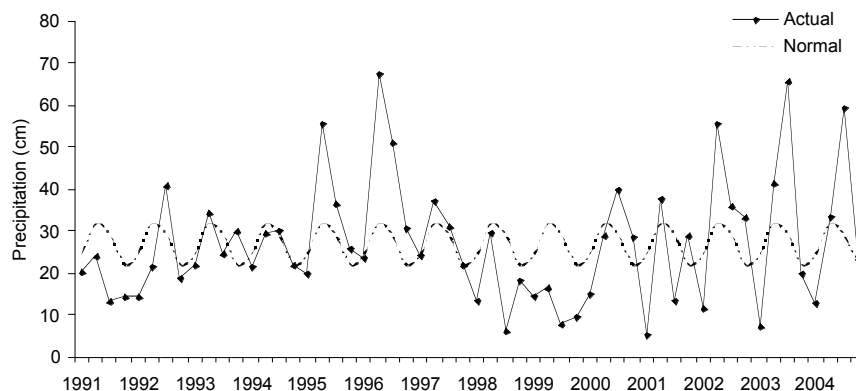


Figure 3. Quarterly-annual normal and recorded precipitation totals for Columbus, Ohio based on data collected from the Ohio Agriculture and Development Center weather station (www.oardc.ohio-state.edu/centernet/weather.htm). Precipitation totals reported for January-March, April-June, July-September and October-December of 1991-2004.

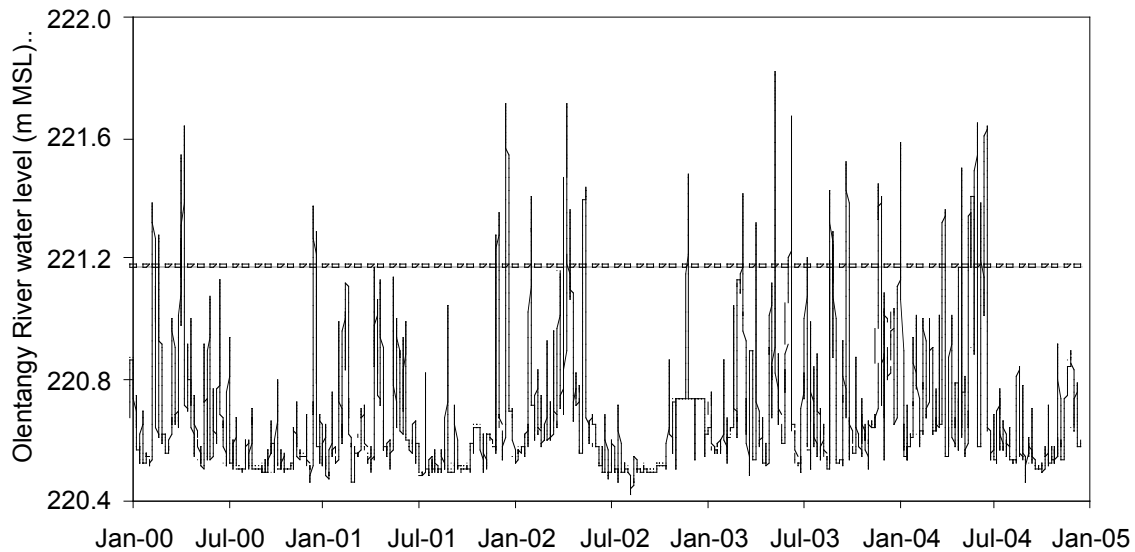


Figure 4. Post-restoration hydrograph of river water levels (m above MSL) for the Olentangy River for 2001-2004 based on data collected at the Olentangy River Wetland Research Park (Mitsch and Zhang 2004).

Table 1. Synopsis of tree plot environmental variables used for regression analyses with forest productivity.

Plot environmental parameters	Mean (\pm SE)	Range
2004		
No. of floods (total)*	4.4 \pm 0.2	4 - 5
No. of floods (growing season)*	3.4 \pm 0.2	3 - 4
Days connected with the river (total)*	21.1 \pm 2.9	15 - 30
Days connected with the river (growing season)*	17.7 \pm 2.7	7 - 26
2003-2004		
No. of floods (total)*	11.1 \pm 0.6	8 - 13
No. of floods (growing season)*	8.2 \pm 0.6	6 - 10
Days connected with the river (total)*	37.8 \pm 5.8	16 - 56
Days connected with the river (growing season)*	28.8 \pm 4.9	11 - 44
2001-2004		
No. of floods (total)*	16.2 \pm 1.3	10 - 20
No. of floods (growing season)*	11.1 \pm 0.9	8 - 14
Days connected with the river (total)*	54.0 \pm 8.1	22 - 81
Days connected with the river (growing season)*	38.3 \pm 6.0	17 - 57
Mean plot elevation (m above MSL)	221.38 \pm 0.07	221.08 - 221.86
Plot elevation variance	1.15 \pm 0.43	0.21 - 4.67
Mean canopy cover (%)	81.7 \pm 1.3	72.9 - 88.2
Total basal area (cm ² m ⁻²)	39.0 \pm 3.8	27.2 - 65.0

* Flood parameters do not include upland plot #5 which was estimated to have flooded only once (in 2003) from 2001 to 2004.

NOTE: total year consists of 12 months (from preceding Oct - Sept). Growing season is April thru September.

Table 2. Importance value (= rel. density + rel. dominance + rel. frequency) of all tree species identified in the north and south sections of the ORWRP bottomland forest. Dominant species (Impt.value >35) are in bold.

Species (common name)	Importance Value	
	North Sec.	South Sec.
<i>Acer negundo</i> L. (boxelder)	36.6	94.3
<i>Acer saccharinum</i> L. (silver maple)	15.0	8.9
<i>Acer saccharum</i> Marsh. (sugar maple)	7.1	9.2
<i>Aesculus glabra</i> Willd. (Ohio buckeye)	48.5	51.1
<i>Asimina triloba</i> (L.) Dunal (paw paw)	68.0	--
<i>Celtis occidentalis</i> Willd. (hackberry)	46.1	8.1
<i>Fraxinus pennsylvanica</i> Marsh. (green ash)	3.9	6.2
<i>Gleditsia triacanthos</i> L. (honey locust)	--	16.0
<i>Juglans nigra</i> L. (black walnut)	13.8	4.6
<i>Lonicera maackii</i> (Rupr.) Amur honeysuckle	--	7.0
<i>Maclura pomifera</i> (Raf.) (osage-orange)	3.8	--
<i>Morus alba</i> L. (white mulberry)	8.8	7.1
<i>Morus rubra</i> L. (red mulberry)	8.7	6.8
<i>Platanus occidentalis</i> L. (sycamore)	18.9	20.4
<i>Populus deltoides</i> Bartr. Ex (cottonwood)	11.2	41.3
<i>Prunus serotina</i> Ehrh. (black cherry)	--	5.8
<i>Salix nigra</i> L. (black willow)	--	7.5
<i>Ulmus americana</i> L. (American elm)	9.5	6.0
Total	300.0	300.0

Length of inundation after flooding occurred was not systematically measured, however it was normal for water to rapidly drain from low spots in the bottomland forest after only a few days, depending upon the flood stage, post-flood river levels and season. Winter flood water often froze once in the bottomland and may last for weeks while summer flood waters dried out the quickest (presumably because of enhanced transpiration). Tree plots within the bottomland connected with the river at different river stages with Plots #1, 6, 8 and 10 being the first to flood. Consequently, during minor flood events (between 221.2 and 221.4 m MSL), these plots would connect with the river while the others would not. Approximate river stage at which each plot was flooded was determined and based on hydrograph data, the number of days and flood events affecting each plot was determined for the entire 2004 year and growing season (Table 1).

Bottomland composition

Based on the identified trees >5 cm dbh, a total of 386 trees representing 19 species were accounted for in the bottomland forest plots. A total of 257 of these trees were in the north section (or 1285 trees ha⁻¹) compared to 129 trees in the south section (or 516 trees ha⁻¹). Forest composition was different between the two sections with the north section having a higher proportion (62%) of small

trees (5-10 cm dbh) compared to the south section (44%). Size distribution was fairly even in the south section with subcanopy trees (10-25 cm dbh) constituting 25% of the total and canopy trees (>25cm dbh) at 30%. Subcanopy and canopy trees in the north section constituted 27% and 11%, respectively.

Understory trees in the north section have become dominated by paw paw (*Asimina triloba* L.) to the extent that they have become the more dominant species in terms of importance value (Table 2). Other trees with high importance values in the north section included Ohio buckeye (*Aesculus glabra* Willd.), hackberry (*Celtis occidentalis* Willd.) and boxelder (*Acer negundo* L.). Trees in the south section were dominated by overstory species *A. negundo* and to a lesser extent *A. glabra* and eastern cottonwood (*Populus deltoides* Bartr. Ex).

Aboveground net primary productivity

There was no significant differences detected in ANPP between the north section (807 ± 86 g m⁻² yr⁻¹) and the south section (869 ± 56 g m⁻² yr⁻¹) (Fig. 5). Significantly higher (t=-2.86, df=5, P<0.05) mean litterfall production was detected in the south section (555 ± 32 g m⁻² yr⁻¹) compared to the north section (460 ± 9 g m⁻² yr⁻¹). Unlike litterfall production, wood production was highly variable in the north section ranging between 157-535 g m⁻² yr⁻¹.

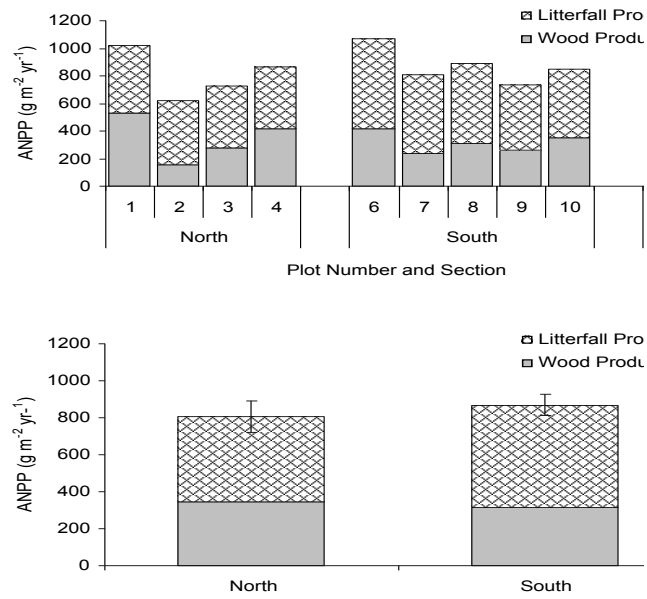


Figure 5. Aboveground net primary productivity (ANPP), including litter-fall and wood production for a) tree plots in the north, south and upland sections, and b) mean (± 1 SE) for north and south section plots for 2004-05. Error bars for the section means represent standard error for ANPP.

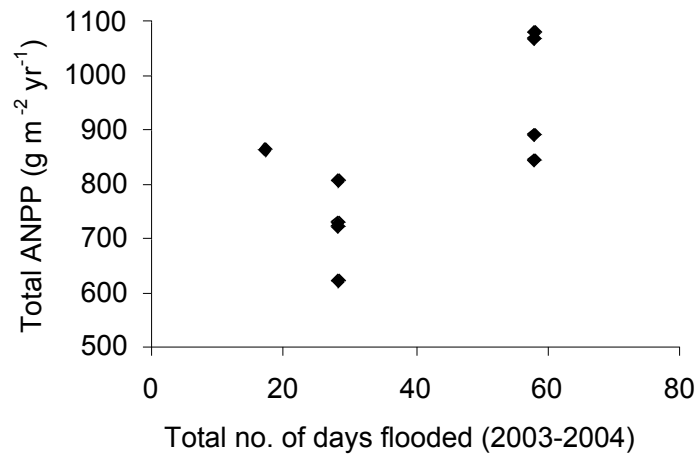


Figure 6. Linear relationship between the number of days flooded (2003-2004) and aboveground net primary productivity for experimental plots in 2004.

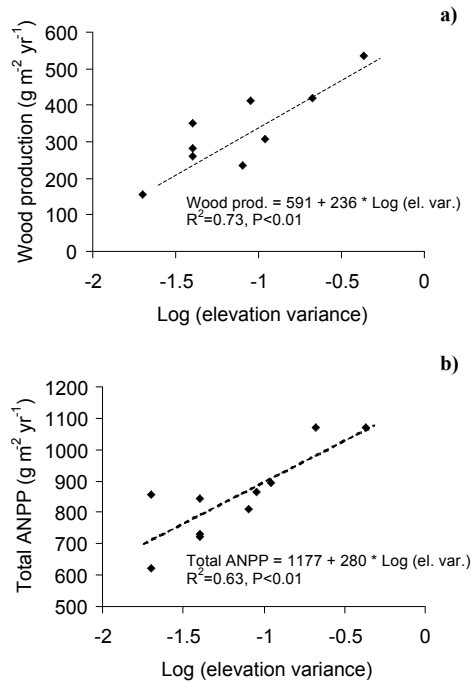


Figure 7. Linear relationship between topographic variability (log-transformed elevation variance) and a) aboveground net primary productivity and b) wood production for experimental plots in 2004-05.

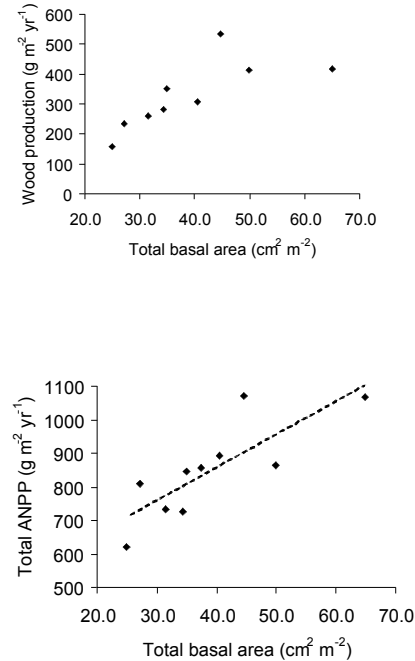


Figure 8. Linear relationship between total tree basal area and a) aboveground net primary productivity and b) wood production for experimental plot data in 2004-05.

Table 3. Results of paired t-tests for mean (± 1 SE) basal area increment (BAI) (% and cm² yr⁻¹) of canopy trees pre- and post-restoration. NS denotes non-significant p-value.

Section (n)	BAI parameter	Mean basal area increment		Paired t-test	
		Pre-restoration (1991-2000)	Post-restoration (2000-2004)	T-value	P
North (n=17)	%	4.3 \pm 0.6	3.3 \pm 0.6	2.99	0.009
	cm ² yr ⁻¹	33.5 \pm 4.6	30.8 \pm 4.0	0.90	NS
South (n=25)	%	3.0 \pm 0.4	2.3 \pm 0.2	2.28	0.032
	cm ² yr ⁻¹	28.5 \pm 3.6	27.4 \pm 3.7	0.41	NS
Upland (n=7)	%	3.0 \pm 0.5	3.8 \pm 0.6	2.30	NS
	cm ² yr ⁻¹	24.8 \pm 3.6	24.6.0 \pm 4.9	0.04	NS

No significant difference was detected between mean wood production in the north (346 ± 82 g m⁻² yr⁻¹) and south section (314 ± 33 g m⁻² yr⁻¹). Productivity in Plot #5 (which was converted to an upland plot based on its elevation) had ANPP, litterfall and wood production (855, 544 and 311 g m⁻² yr⁻¹, respectively) that was comparable to plots in the adjacent south section.

Predicting ANPP, litterfall production and wood production

Using plot-level flooding and productivity data, a significant relationship between the total number of days flooded in 2004 (October 2003 - September 2004) and ANPP was detected ($R^2=0.44$, $P=0.050$). Furthermore,

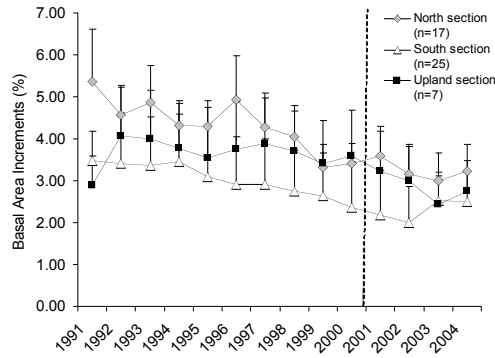


Figure 9. Mean (± 1 SE) BAI (%) for bottomland canopy trees from the north, south and upland sections from 1991 to 2004. The dashed line represents pre- and post-restoration periods.

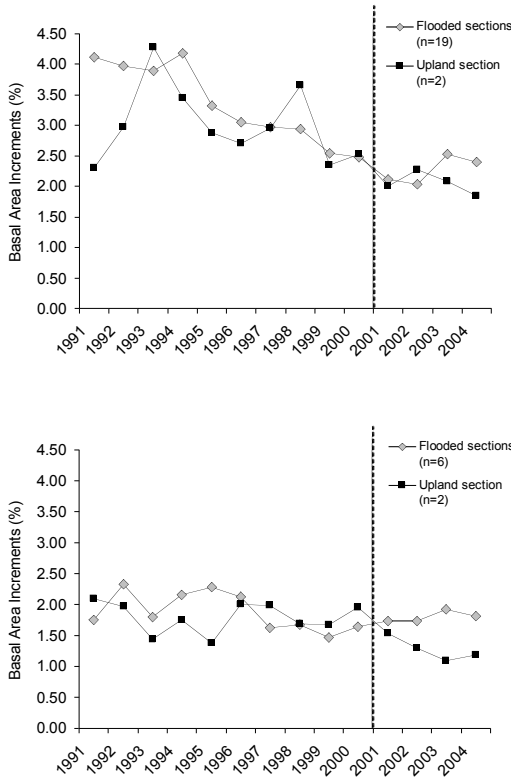


Figure 10. Mean BAI(%) for a) boxelder (*Acer negundo* L.) and b) Ohio buckeye (*Aesculus glabra* Willd.) bottomland canopy trees in the flooded and upland sections from 1991 to 2004. The dashed line represents pre- and post-restoration periods.

when flooding based on river levels from the preceding year were added (2003 and 2004), significant relationships were detected between ANPP and the total number of flooded days ($R^2=0.48$, $P=0.040$, Fig. 6) and the total number of days flooded in the growing season ($R^2=0.46$, $P=0.040$). Regression analyses determined that none of the flood frequency parameters calculated had an influence on the separate components of ANPP (litterfall or wood production).

Both ANPP and wood production were significantly influenced by plot topographic variability (elevation variance) (Fig. 7) and total tree basal area ($\text{cm}^2 \text{m}^{-2}$) (Fig. 8). Elevation variance data was log-transformed to meet normality assumptions. No significant relationships were detected between any predictor variables and litterfall production. A synopsis (range, mean and standard error) of all predictor variables used to predict forest productivity through regression analysis is provided in Table 1.

Tree-ring analysis for BAI

Comparing the mean BAI (%), canopy trees in the north and south section decreased in mean increment size after the restoration ($P>0.01$ and $P=0.03$, respectively, Table 3). However, no significant changes were detected in actual

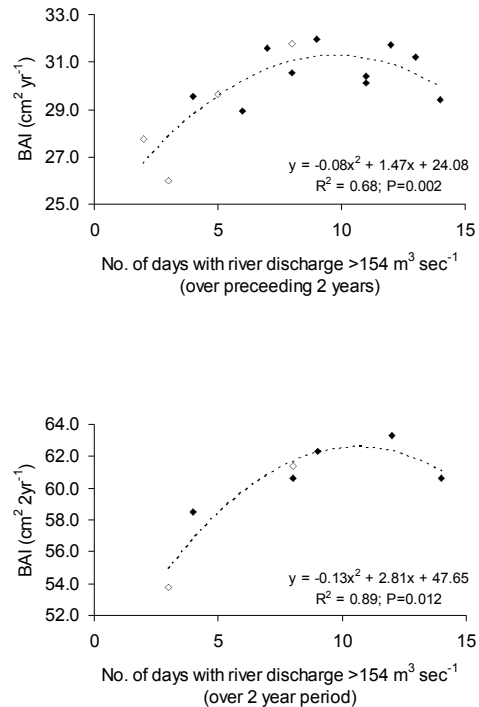


Figure 11. Polynomial relationship between a) the number of days of river discharge $>154 \text{ m}^3 \text{sec}^{-1}$ over the preceding two years and basal area increment (BAI) and b) the number of days of river discharge $>154 \text{ m}^3 \text{sec}^{-1}$ and BAI over 2-yr periods from 1991-2004. Open symbols represent post-restoration years.

Table 4. Results of paired t-tests for mean (± 1 SE) basal area increment (BAI) (% and $\text{cm}^2 \text{yr}^{-1}$) pre- and post-restoration for boxelder (*Acer negundo* L.) and Ohio buckeye (*Aesculus glabra* Willd.). NS denotes non-significant p-value.

Species (n=)	BAI parameter	Mean basal area increment		Paired t-test	
		Pre-restoration (1991-2000)	Post-restoration (2000-2004)	T-value	P
<i>A. negundo</i> (n=19)	%	3.2 \pm 0.3	2.3 \pm 0.2	2.75	0.013
	$\text{cm}^2 \text{yr}^{-1}$	29.1 \pm 3.8	27.7 \pm 3.5	1.38	NS
<i>A. glabra</i> (n=6)	%	1.9 \pm 0.4	1.8 \pm 0.3	0.25	NS
	$\text{cm}^2 \text{yr}^{-1}$	14.1 \pm 4.5	14.8 \pm 3.9	-0.35	NS

annual BAI ($\text{cm}^2 \text{yr}^{-1}$), suggesting that trees maintained consistent wood production since 1991 while increasing in age. No significant changes in BAI (% or $\text{cm}^2 \text{yr}^{-1}$) were detected in upland trees. It was noted during the analysis that 5 of the largest tree specimens (all >75 cm dbh) had consistently low BAI (%) values that had an excessive influence on mean comparisons and trend analyses, and were therefore omitted. We presumed that these older trees had reached an age where a high proportion of gross production is used for maintenance metabolism (Kimmins, 1987) and were unlikely to provide a growth response to changing moisture conditions.

Evaluation of trend analyses showed that none of the sections had an abrupt shift in basal growth immediately after hydrologic restoration (Fig. 9). However, canopy trees in the south section showed increased radial growth in 2003 and 2004 compared to a trend of consistent decline in BAI(%) since 1994. Trees in the north and upland sections showed a slight increase of BAI(%) in 2004, however conditions in both sections during pre-restoration years were more variable making this shift difficult to assess.

Two of the most dominant trees in the bottomland forest (*A. negundo* and *A. glabra*) were evaluated separately to see if responses between species were different. Because similar trends were detected in *A. negundo* between the north and south sections, these trees were pooled. No canopy-sized *A. glabra* occurred in the north section plots. Like trees in the north and south sections, *A. negundo* had a significantly lower mean BAI (%) after the restoration ($P>0.05$) but with no significant change in BAI ($\text{cm}^2 \text{yr}^{-1}$) (Table 4). Trend analyses indicated that unlike canopy specimens in the upland section, *A. negundo* trees in the flooded sections may have responded positively to the restoration based on the increased BAI (%) in 2003 and 2004 (Fig. 10a). *A. negundo* trees in the upland sections seemed to follow a basal growth trend that extended back to 1991.

The BAI (% and $\text{cm}^2 \text{yr}^{-1}$) of *A. glabra* canopy trees were not significantly different between pre- and post-restoration years (Table 4). Upland and flooded specimens had similar BAI (%) extending back to 1991 (Fig. 10b). After 2000, there was a separation between the upland and flooded trees, however BAI trajectories did not shift substantially in the post-restoration period.

Predicting basal growth

A significant relationship was detected between the total number of days where the river discharged at high-flood stage ($>154 \text{ m}^3 \text{sec}^{-1}$) and BAI ($\text{cm}^2 \text{yr}^{-1}$) when analyzed using the preceding 2-yr river data (Fig. 11a). Similarly, a significant relationship was detected between the number of high-flood days over a 2-yr period and the corresponding 2-yr BAI ($\text{cm}^2 \text{yr}^{-1}$) (Fig. 11b). No significant relationships were detected between the number of days or events of discharge and the BAI for that corresponding single year. A significant relationship between the total number of high-flood discharge events and 2-yr preceding river data was also detected ($R^2=0.54$, $F=13.93$, $P=0.003$), but the number of events was less predictive than the number of days. No other significant relationships between BAI and river discharge were detected. In all cases, BAI (%) data showed indications of autocorrelation and therefore were omitted from consideration in favor of BAI ($\text{cm}^2 \text{yr}^{-1}$).

Discussion

Bottomland productivity

One of the most commonly cited benefits associated with the hydrologic restoration of a bottomland forest is the likely enhancement in productivity. Based on the results of this study there is some evidence to suggest that after only four years, there was an increase in bottomland

productivity. In terms of ANPP, we found no significant differences between the north ($807 \pm 86 \text{ g m}^{-2} \text{ yr}^{-1}$) and south ($869 \pm 56 \text{ g m}^{-2} \text{ yr}^{-1}$) sections. This was important because using productivity data from plots comparable to our study, Cochran (2001) found that ANPP in the north section ($531\text{--}641 \text{ g m}^{-2} \text{ yr}^{-1}$) was significantly lower than the south ($793\text{--}1033 \text{ g m}^{-2} \text{ yr}^{-1}$). This suggests that the north section has increased in productivity since the restoration activity occurred. The biggest difference between pre- and post-restoration productivity in the north section was in mean wood productivity which, in 2004 ($346 \text{ g m}^{-2} \text{ yr}^{-1}$, this study) was nearly triple that estimated in 2000 ($117 \text{ g m}^{-2} \text{ yr}^{-1}$, Cochran, 2001). However, the change in wood productivity conflicts somewhat with our tree canopy ring-analysis data which saw relatively consistent basal area growth ($\text{cm}^2 \text{ yr}^{-1}$) between pre- and post-restoration years in the north section. Given the high variability of wood production estimated for plots in the north section, plot location may have greatly influenced estimates in both studies. Cochran (2001) only used 2 plots ($20 \times 25\text{m}$) in the north section directly affected by the levee, compared to 4 plots used in this study. Therefore we conclude only tentatively that ANPP has increased in the north section.

Based on estimates by Cochran (2001), ANPP in the north section had clearly exceeded its pre-restoration range while in the south section ANPP was still within the pre-restoration range. Furthermore, the ANPP range seen at the bottomland forest was still below what has been recorded at other sections of the Olentangy River. At two other unrestricted bottomland hardwood forests upriver from the ORWRP (both within 12 km), forest ANPP was estimated at 1283 ± 56 and $1297 \pm 302 \text{ g m}^{-2} \text{ yr}^{-1}$ (Cochran, 2001). The ANPP range seen at the ORWRP bottomland also seems to be lower than what has been observed at most other bottomland forests in the region. Mitsch et al. (1991) found ANPP at 1280 and $1334 \text{ g m}^{-2} \text{ yr}^{-1}$ in two hardwood bottomland forests along the Ohio River in western Kentucky. ANPP for a floodplain forest in Illinois was estimated at $1250 \text{ g m}^{-2} \text{ yr}^{-1}$ (Johnson and Bell, 1976). However, Brown and Peterson (1983) found that ANPP at another bottomland forest in Illinois with stagnant water conditions was $960 \text{ g m}^{-2} \text{ yr}^{-1}$ while a seasonally flooded forest was at $668 \text{ g m}^{-2} \text{ yr}^{-1}$. It seems that in terms of long-term productivity, the ORWRP bottomland may still have an opportunity to increase.

Although leaf productivity was significantly higher at the south section, it appeared that wood production was more the responsive component affecting ANPP based on the wide ranges observed at the ORWRP (Fig. 5). This in contrast to other studies (Burke et al., 1999) which found leaf production to be more variable. Part of the reason that litterfall was more consistent between plots may have been the frequent occurrence of paw paw (*A. triloba*) in north section plots. Although these plots had less canopy-tree cover and overall basal area, there was a large contribution of litterfall provided by subcanopy *A. triloba* which produced a dense cover of large leaves.

Relationship between bottomland productivity and flooding

Although plot ANPP was predicted by the number of days each was flooded in 2004, the best relationships were found using flood data added from 2003 and 2004. The results of these analyses confirmed that surface water flooding was an important factor in determining forest productivity and also suggests that flood events may influence productivity beyond the year they occur. Similar patterns were revealed using river discharge to predict basal tree growth (see section below). It is possible that this delayed response represents the time it takes for deposited nutrients to desorb from sediment and mineralize from matter and become available. The decomposition of organic matter, the desorption of nutrients from sediment and the alteration of soil chemistry are all factors that dictate nutrient availability in bottomland soils (Mitsch and Gosselink, 2000). The rates of these processes are eventually dependent upon environmental conditions including hydrology and climate. Therefore if it takes several months for ecological processes to make nutrients available, nutrients from material deposited in the spring and early summer (when most flooding traditionally happens) may not become available to plants until the subsequent growing season.

Using regression analyses, total ANPP and wood production were significantly influenced by total basal area and topographic variability (elevation variance). It was no surprise that existing basal area influenced productivity however elevation variance was one of the least considered predictor variables at the onset of this study. Floodplain bottomlands can have naturally diverse topographies consisting of repeated ridges, swales and meandering scrolls (Leopold et al., 1964). The influence of topography has been demonstrated on forest productivity in the southern Appalachian (Bolstad et al., 2001), on riparian plant diversity in Alaska (Pollock et al., 1998) and canopy gap regimes in a Texas bottomland forest (Almquist et al., 2002), however there is little information pertaining to its influence on bottomland tree productivity. A diverse topography such as that of a ridge-and-swale would perhaps allow the greatest interface between flood waters and trees on slightly elevated ground. In the case of the ORWRP bottomland, topographic variability was provided by swales and ridges in the south section, however in the north section it was provided by the old fill material from the remnant levee. The influence of topography on bottomland productivity is an interesting result from this study and we would encourage future bottomland research to consider this component.

Forest basal growth before and after restoration

Evaluating canopy tree cores, we did not find an occasion where radial tree growth made an immediate and clear response to the restored hydrology. Given that the north section was a more complete restoration (hydrology was only enhanced in the south section) we were expecting to

see a positive response to the restored hydrology. However, compared to the other sections, only the south section showed a potential response. The change in BAI (%) seen at the south section in 2003 and 2004 was interpreted to be a more significant shift because it represented a clear break in a very consistent growth trend dating back to 1994. An increase was detected in the north section in 2004, however given the modest size of the increase, the more sporadic growth trend leading up to it, and that upland trees showed a similar increase; this change cannot be considered conclusive. It may be that because the south section trees were exposed to occasional flooding prior to the restoration work, trees in this section were better conditioned to the altered hydrology. Assuming that the increased flooding has been a stress to trees, when stressors are introduced more gradually, trees can generally make the physiological adjustments to protect themselves much more than if the stressor is introduced rapidly (Kozlowski and Pallardy, 2002). The canopy tree response in the south section may have been in response to the high inflows that occurred in 2003 and 2004, or perhaps more likely, it may be a lag response to the new hydrology. This would not be unprecedented, as lags in forest response have been documented in the case of other habitat improvements. Jones and Thomas (2004) found that in Ontario forest stands dominated by sugar maple (*Acer saccharum* Marsh), peak growth enhancement in response to canopy gaps did not occur until 3-5 years later. Given the shift in hydrology is even more substantial in the north section it may take longer for trees there to positively respond. Anaerobic conditions caused by flooding may have been exacerbated in this section where flooding was previously rare.

A. negundo was the dominant tree in the south section and therefore its trend in BAI (%) over time (Fig. 10a) was similar to that seen for all south section trees (Fig. 9). However, *A. negundo* specimens tended to respond similarly in the north section as well. The response of trees in the flooded sections since the restoration is in contrast to upland specimens where BAI (%) maintained the same trend set before the restoration occurred. The physiology of *A. negundo* may make it well adapted to changing water conditions as it has been shown that its net photosynthesis can be resilient to seasonal changes in soil water potential (Foster, 1992). *A. glabra* on the other hand did not show a substantial response although its BAI (%) has not declined during the post-restoration period as the upland specimens have. Nevertheless, this tree tends to occur in moist soils and while it is considered resistant to saturation, it is a facultative upland species and might be less resilient to prolonged anaerobic conditions.

Basal growth in response to flooding

Based on the results of this study, there is evidence that flooding may have a lagged effect on tree growth. In both scenarios where river discharges from the current and previous years were added, there was a significant relationship between the number of days with high-flood

discharge and BAI ($\text{cm}^2 \text{yr}^{-1}$). Given the pre-restoration exclusion of bank-full flood waters it is not surprising a relationship was only detected using the high-flood events, and as indicated in Figs. 11a and b, the bottomland forest was still responding to these high-flood occurrences during the post-restoration years. The evidence of a lagged response by bottomland canopy trees to flooding has been rarely documented however it isn't unexpected given the amount of other circumstances where forests have shown a lagged response in growth. Factors such as climate (Fritts, 1976; Camill and Clark, 2000), newly formed canopy gaps (Jones and Thomas, 2004) and the removal of shelterwoods (Holgen et al., 2003) have all been shown to induce a lagged response on tree basal growth.

Significant regressions using current- and previous-year river discharge data indicated that basal tree growth occurred at an optimal number of high-water discharge days (~10) suggesting that trees are benefiting from a nutrient subsidy to a point. After about 10 high-flood discharge days, the bottomland may no longer be nutrient limited and anaerobic conditions may have reduced productivity. It is important to point out that in the 2-yr periods where high-flood discharge exceeded 10 days, the decrease in basal growth was marginal compared to those years where floods events were scarcer. The general relationship seen in this case is not unprecedented. Golet et al. (1993) showed that the highest tree basal growth at red maple (*Acer rubrum* L.) swamps in Rhode Island occurred at intermediate annual water levels. The results from this study support findings such as these and demonstrate the push-pull influence that flooding has on forest productivity.

The fact that flooding throughout entire years (and not just the growing seasons) was the best predictor of basal growth supports the idea that these trees were responding more to a nutrient subsidy and less to the anaerobic stress of flooding. If flooding stress was more important, we would have expected a relationship with BAI to manifest during the growing season. However, as seen in other studies, it is likely that the anaerobic stress caused by flooding in the growing season was negated by a nutrient subsidy, and therefore a relationship between growing season flood occurrence and BAI was unapparent. Furthermore, it appears that trees are responding to sediment and nutrient deposition occurring year-round. Through the work of Zhang et al. (2006) and personal observations, it has been shown that these flood events can deposit significant amounts of material into the bottomland forest and the amount of material, sediment and nutrients available to trees may ultimately be dependent upon the frequency of major flood events in the preceding years.

Conclusions

Hydrologic restoration of the ORWRP bottomland forest was conducted in 2000 and as a result, the north section has received direct surface flows from river floods and the south section has increased its surface flow and frequency.

The two sections were similar in ANPP, but compared to previous estimates conducted before the restoration, the north section has increased its mean ANPP since the restoration occurred. No abrupt and clear changes in canopy tree basal growth has occurred since the restoration occurred; however since 2003, trees in the south section of the bottomland have shifted from a continuous trend of declining BAI (%) extending back about ten years. Evaluating BAI and river discharge data since 1991, these results suggest that for a two-yr period, optimal basal growth will occur when ~10 days of high-flood discharge occur during that period. These results also suggest that basal growth in response to flooding is lagged by at least one year as no relationships were detected between tree basal growth and concurrent flooding over one year. The lack of any significant relationship between tree basal growth and flooding in the growing season suggests that sediment and nutrient deposition are likely more important to forest productivity than the stress caused through flooding.

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